

Studies on the littoral seaweed epifauna of St. Croix Island. I. Physical and biological features of the littoral zone

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The physical and biological features of the littoral zone of St. Croix Island are described as a prelude to studies on the seaweed epifauna. Wave action is the most important physical variable and shore community structure is markedly influenced by the differing degrees of wave action around the island. Sheltered, moderately exposed, exposed and very exposed littoral communities are distinguished and at three transects the zonation of the macrofauna and the percentage cover of the littoral seaweeds is determined. Seasonal variation, particularly in the seaweed *Porphyra capensis*, is documented, seaweed cover is related to biomass and energy values for 14 littoral seaweeds are determined.

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Die fisiese en biologiese kenmerke van die St. Croix Eiland kusgebiedsone word beskryf as 'n inleiding tot studies van die seewier epifauna. Golwerking is die mees belangrike fisiese veranderlike en kusegemeenskapstruktuur word opvallend beïnvloed deur die verskillende grade van golfwerking. Beskutte, gematig blootgestelde, en baie blootgestelde kusgebied gemeenskappe word gekenmerk en in drie seksies word die sonasie van die makrofauna en die persentasie dekking van kusgebiedseewiere bepaal. Seisoenale variasie, veral in die seewier *Porphyra capensis* is bewys, seewierdekking hou verband met biomassa, en energiewaardes is bepaal vir 14 kusgebiedseewiere.

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St. Croix Island (33°48'S, 25°46'E) in Algoa Bay is very suitable for ecological studies as it is relatively undisturbed and free from human exploitation. The marine and terrestrial biota of the island is at present being investigated by the University of Port Elizabeth.

The coast of South Africa has been divided into west, south and east coast faunistic provinces on the basis of the littoral biota (Stephenson 1944; Day 1969; Stephenson & Stephenson 1972) and St. Croix Island falls into the south coast region. The biota on rocky shores in and near Algoa Bay have been divided into four principal zones namely, littorina, balanoid, cochlear and sublittoral fringe (Stephenson, Stephenson & Bright 1938). Preliminary work on the fauna and flora of St. Croix Island (McLachlan & McLachlan 1974; McLachlan 1974; De Villiers 1976) revealed that the littoral biota of the island is similar in both composition and zonation to that of the nearby mainland coast.

This paper, the first in a series, summarizes available information on the physical factors affecting the St. Croix littoral zone and presents data on the distribution, zonation and abundance of the littoral seaweeds as a precursor to studies on the seaweed epifauna. Notes are also given on the littoral macrofauna.

Physical features of the St. Croix littoral zone

St. Croix Island, the largest of three offshore islands in Algoa Bay, is an outcrop of Table Mountain Sandstone surrounded by water 20 m in depth (Fig. 1). The Island (Fig. 2) is about 550 m long and 250 m wide with a very regular north coast, a south coast incised by numerous gullies and a littoral perimeter of 3 180 m. The semidiurnal tides of Algoa Bay, with a mean spring range of 1,61 m and a mean neap range of 0,51 m (South African Navy 1977), regularly expose the littoral zone to both atmospheric and marine conditions.

Although meteorological reports do not reveal the actual conditions close to the surface on the shore they do give some basis for comparisons (Lewis 1972). To this end the average monthly air temperatures recorded at the Port Elizabeth airport (25 km south-west of St. Croix) are given in Fig. 3. St. Croix experiences a warm temperate climate with a mean annual temperature of 17 °C, a daily range of

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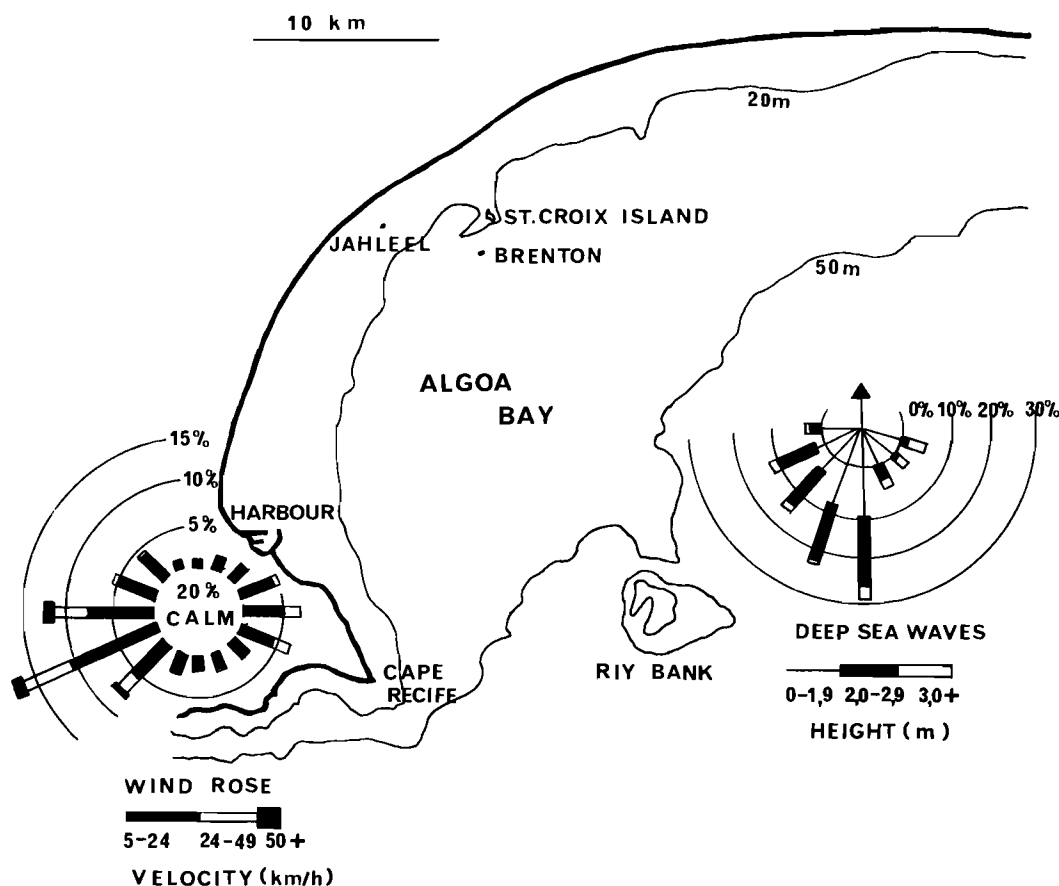


Fig. 1 Map of Algoa Bay, showing the offshore islands, a wind rose for an average year (Port Elizabeth airport) and a deepsea wave rose (Cape St. Francis).

about 10 °C and an extreme annual range from freezing point to 40 °C. The annual rainfall of about 600 mm occurs throughout the year with spring and autumn peaks.

The wind rose for an average year, compiled from records at the Port Elizabeth airport, indicates that winds are chiefly from the south-west (Fig. 1). In summer south east winds are frequent and they increase in velocity in the afternoons. On winter mornings, north-west winds which abate before midday or swing to the south-west and intensify in the afternoon, are common. The waters of Algoa Bay are influenced by the warm Agulhas current which flows in a south-westerly direction along the east coast of South

Africa, following the continental shelf (Pearce & Bang 1977). The inshore waters are principally affected by an inshore counter current which is cooler and more fertile than the Agulhas current. A regular seasonal temperature pattern occurs (Fig. 3) with an extreme annual range from 11 °C during upwelling to 25 °C when the Agulhas

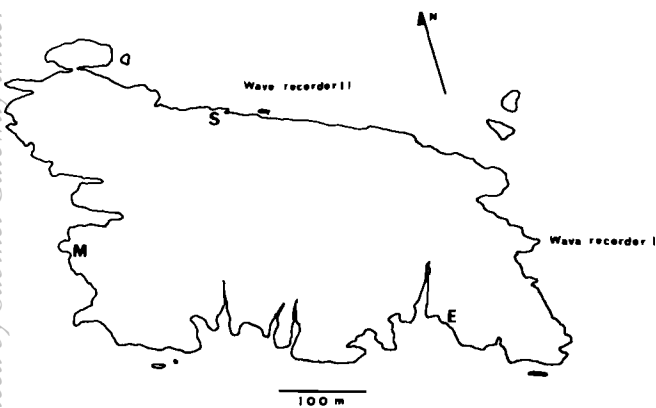


Fig. 2 Map of St. Croix Island, showing positions of wave recorders I and II and Transect sites S, M and E.

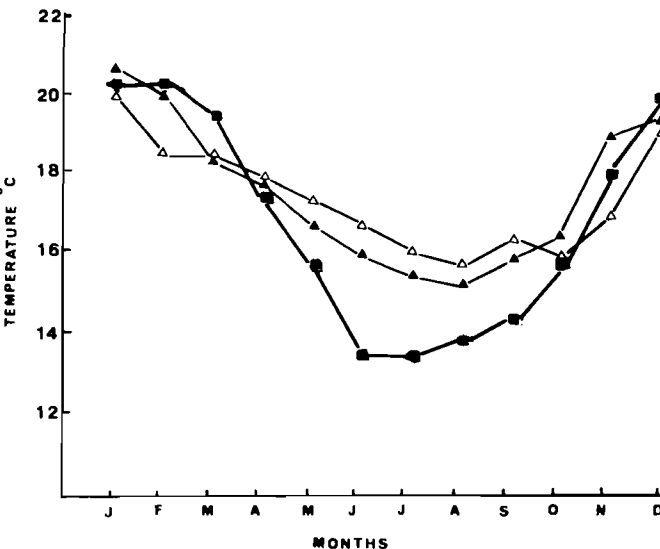


Fig. 3 Mean monthly air temperatures from the Port Elizabeth airport (1937-1972) and sea temperatures in Algoa Bay.

- Mean monthly air temperature;
- △-△ Mean offshore temperature from Maritime weather charts (Jan. 1975-Sept. 1977);
- ▲-▲ Mean surf temperatures from Humewood Beach (1972-1977).

meanders inshore.

Off the Cape coast most waves approach from the south and south-west as they are generated by storms moving from west to east in the depression belt usually located to the south of the African continent (Darbyshire & Darbyshire 1964). Deepsea wave recordings (Ashly, Harper & Van Schaik 1973) from Cape St. Francis, 60 km west of Algoa Bay, are summarized in Fig. 1. These southerly swells are however deflected to the south east on entering Algoa Bay due to refraction of waves by Cape Recife and the shallow Ruy Bank in the southern part of the bay. An engineering feasibility study on St. Croix (Soros Ass. Int. 1973) compared wave heights at Cape St. Francis with those off the east and north coasts of St. Croix (Fig. 2) and a graphical interpretation of their results is given in Fig. 4. This shows how wave height decreases markedly within the bay with the shelter provided by the surrounding land and finally the island itself.

The amount of wave action experienced by any shore depends partly on its position relative to the open sea and prevailing winds, and partly on its topography (Lewis 1972). The north coast of St. Croix is protected from the prevailing winds and swells, the south and east coasts face the open sea and the west coast is exposed to the prevailing winds although the fetch is only about 5 km.

The amount of wave action thus varies around the island.

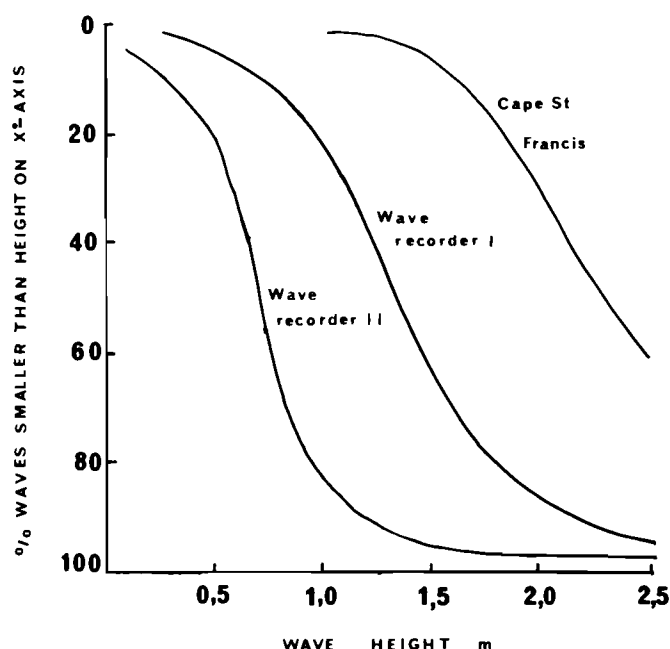


Fig. 4 Comparison of wave height between Cape St. Francis and the exposed (I) and lee sides of St. Croix Island (II) from Nov. 1970–April 1971 (after Soros Ass. Int. 1973).

Using a Savonius rotor or 'turbulometer', as developed by Field (1968) relative wave action was measured at three sites, S, M, and E, on St. Croix (Fig. 2).

At the three transect sites permanent concrete blocks with bolts for the attachment of the rotor were affixed to the rock surface on the midshore. Recordings of wave action were made as the waves surged over the rotor for 15 min before the predicted time of spring high tide on three successive days in September 1977.

Waves that did not reach the rotor were given a zero reading. Results are given in Table 1 and t-tests showed significant differences ($p < 0.01$) between the means of recordings at the three sites. Site E on the south coast experienced the most wave action, Site M on the west coast was moderately exposed and Site S on the north coast was subject to the least wave action although water movement there was still considerable. Waves approached Site E at a frequency of about 5 min^{-1} whilst at the other two sites a higher frequency was recorded, probably due to rocks and promontories complicating the wave pattern.

The localized effects of wind and waves thus result in variable exposure to wave action around the island, from very exposed on the south and east coasts to moderately exposed on the west coast and relatively sheltered on the north coast. The small size of St. Croix eliminates many of the factors influencing distribution and zonation of littoral organisms on rocky shores (e.g. climatic factors, sea temperature, tides and substrate) and wave action can be regarded as the most important physical variable in the St. Croix littoral zone.

Biological features of the St. Croix littoral zone

Methods

The rocky shores at the three sites (S, M and E in Fig. 2) which differed in exposure to wave action were surveyed to the lowest level accessible at low water spring tide using a tape measure and spirit level. No bench mark occurs on St. Croix but by recording the height of the tide relative to topographical and biological features at the transect sites at specific times and then correlating these levels with tidal heights recorded at the same times on a gauge at the Port Elizabeth harbour, the level of Chart Datum on the shore was established. The distribution of the dominant littoral macrofauna around the island was noted and the upper and lower limits of occurrence of the animals at the three transects were recorded.

A PVC tubing frame (25 cm × 25 cm) which could be moved along two ropes spanning the shore was used to determine the area of shore covered by each species of seaweed. The percentage of total quadrat area covered by each species of seaweed within the frame was estimated visually

Table 1 Wave action at three sites at St. Croix Island measured, using a 'turbulometer'. S.D. = Standard deviation

Recording site	Transect S	Transect M	Transect E
Date	26 Sept. 1977	27 Sept. 1977	25 Sept. 1977
Time	14h51–15h06	15h23–15h38	14h18–14h33
No. of waves recorded in 15 min	100	99	77
No. of waves recorded by rotor	98	72	70
Mean of all recordings (rotations min^{-1})	4.92 (3.51 S.D.)	6.01 (6.98 S.D.)	9.19 (6.40 S.D.)
Mean of all positive recordings	5.02 (3.48 S.D.)	8.26 (6.95 S.D.)	10.11 (5.98 S.D.)
Mean no. of waves/min	6.66 (0.90 S.D.)	6.60 (1.06 S.D.)	5.13 (1.25 S.D.)

and a continuous transect series of such coverage estimations was made at each site during the summer of 1975/1976. At Transect S, which is sheltered from direct wave action, the algal coverage of the sublittoral fringe was determined in a similar manner using SCUBA equipment.

At Transects S and M algal coverage determinations were repeated in winter 1976 to determine if there were any seasonal trends in the seaweed communities. Inclement weather conditions and very rough seas prevented quantitative monitoring of Transect E but at regular monthly intervals from July 1976 to October 1977 any observed differences in the seaweed communities were noted.

The relationship between percentage cover and biomass for each algal species was determined in order to quantify results of seaweed epifauna studies. This was done by placing the 25 × 25 cm frame at a convenient spot on the shore and determining the coverage of a specific seaweed. All the specimens of this seaweed were then removed from within the frame with a paint scraper and collected in a polythene bag. In the laboratory the seaweed was thoroughly rinsed in fresh water to remove salt and associated animals and dried at 90 °C for 24 h. Duplicate energy content determinations were made on these dried seaweeds using an adiabatic bomb calorimeter. It was necessary to add benzoic acid to some of the samples and an endothermy correction of 586 J/g CaCO₃ was made for the coralline algae (Paine 1966) on the assumption of a 70 % CaCO₃ content. Percentage ash was determined by ashing duplicate samples of algae at 450 °C for 4 h in a muffle furnace.

Results

The profiles of the rocky shores at the three transect sites are given in Figs. 5, 6 and 7. The north-facing Transect S is slightly steeper than the other two and has a small pool on the upper shore. Both Transects M and E, although on the west and south coasts respectively, are west facing.

On the upper shore of Transect S (Fig. 5) *Littorina knysnaensis* is very abundant and *L. africana* occurs too. The small barnacle *Chthamalus dentatus* is very numerous in the upper balanoid zone. *Octomeris angulosa* and *Tetracelita serrata* occupy the rest of the balanoid zone with *Patella granularis* and clumps of *Perna perna* interspersed among them. A *Patella cochlear* zone occurs on the lower shore with *Pyura stolonifera* evident on the sublittoral fringe.

The upper shore of Transect M (Fig. 6) is occupied by littorinids and *C. dentatus* though the latter is not as numerous as at Transect S. *O. angulosa* is abundant but *T. serrata* is rare on rock surfaces facing the sea. *Thais* sp. and *P. granularis* occur on the mid shore as well and *P. perna* and *P. cochlear* are abundant on the lower shore. There is an extensive sublittoral fringe population of *P. stolonifera* and dense beds were observed when diving near this transect.

Littorinids and *C. dentatus* are scarce at Transect E (Fig. 7) and *T. serrata* is virtually absent. *O. angulosa* is very abundant and large individuals occur. Distinct *P. perna* and *P. cochlear* zones are evident on the lower shore. *P. granularis*, *Thais* sp. and *Burnupena lagenaria* can be found amongst the barnacles and *Haliotis spadicea*, *Parechinus angulosus*, *Asterina exiqua* and other *Patella* species

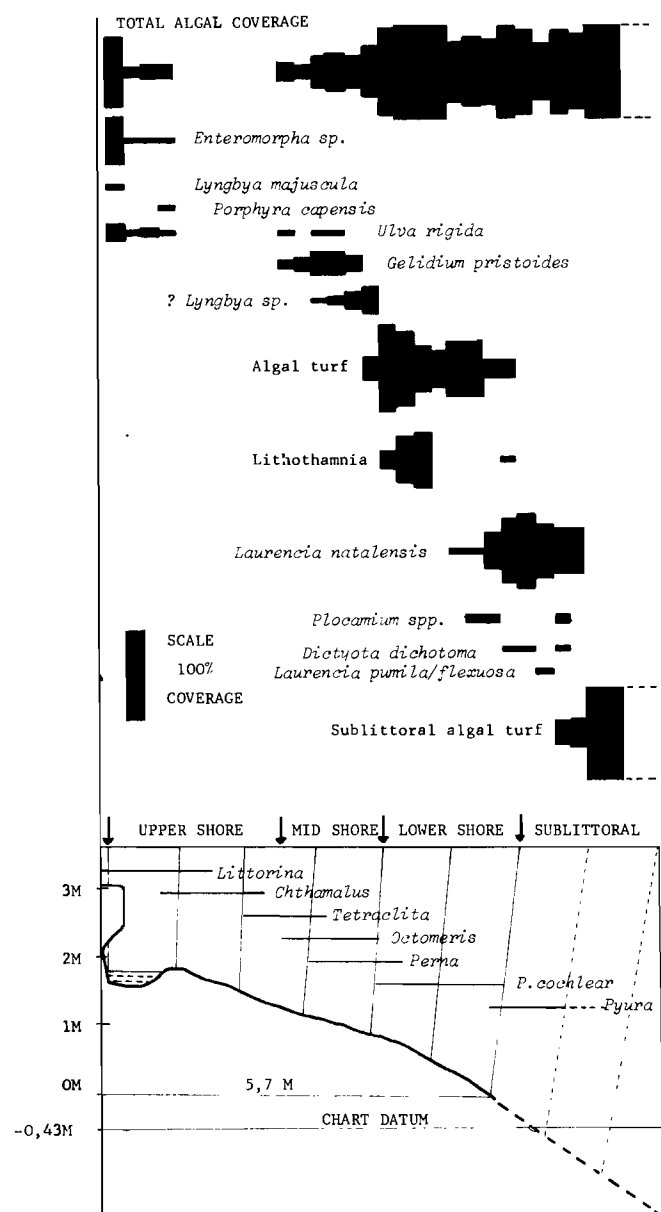


Fig. 5 Rocky shore profile, algal coverage and distribution of dominant animals at sheltered north facing Transect S.

occur on the lower shore. Dense beds of *Pyura* again occur in the sublittoral fringe. *Gunnarea* and *Pomatoleis* are absent.

Seaweed coverage on the upper shore at Transect S (Fig. 5) is low with *Porphyra capensis* occurring in small amounts and *Enteromorpha* sp. and *Ulva rigida* occurring in pools. The mid shore is dominated by *Gelidium pristoides* and a blue green alga, *Lyngbya* sp. and *Ulva rigida* also occur. The lower balanoid and cochlear zones are covered by lithothamnium and an algal turf from which *Jania* sp., *Corallina* sp., *Laurencia natalensis*, *Ceramium* sp., *Gigartina minima* and *Gelidium* sp. have been identified. *Laurencia natalensis* is prolific on the sublittoral fringe and *Plocamium* spp., *Laurencia pumila* and/or *L. flexuosa* and *Dictyota dichotoma* occur as well. Subtidally another algal turf is found from which *Amphiroa* sp., *Polysiphonia* sp., *Ceramium* sp., *G. minima*, *Laurencia* sp., *Centrocerus* sp., *Acrosorium* sp. and *Pterosiphonia cloiophylla* have been identified. Although Transect S is representative of the dominant flora of the north coast of St.

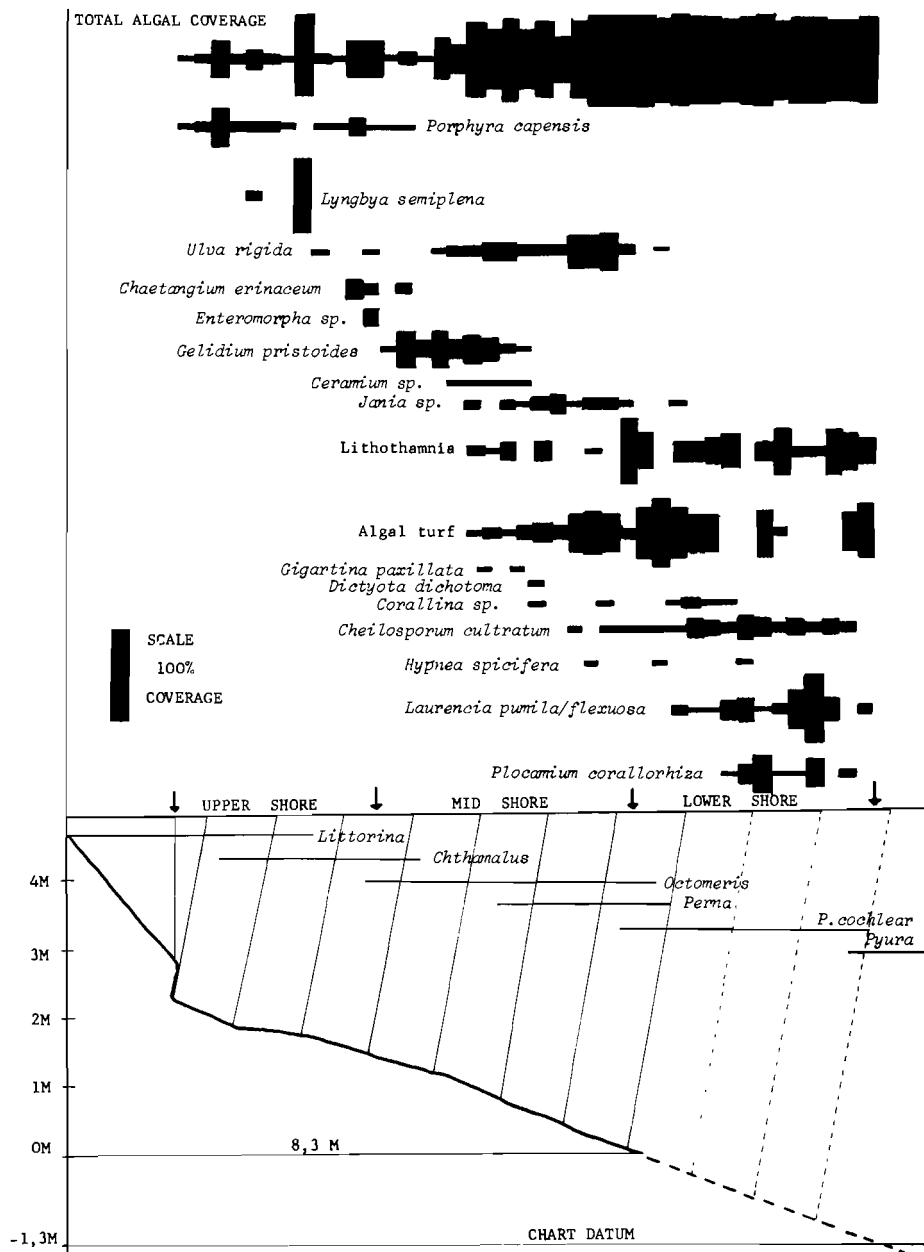


Fig. 6 Rocky shore profile, algal coverage and distribution of dominant animals at moderately exposed Transect M.

Croix a few other species have been found elsewhere in this area. *Bostrichia mixta* occurs in rock crevices on the upper shore, *Chaetomorpha* sp. and *Arthrocardia* sp. have been found in pools and *Caulacanthus ustulatus* also occurs on the mid shore. *Ecklonia biruncinata* was not recorded.

At Transect M (Fig. 6) *P. capensis* and the blue-green alga *Lyngbya semiplena* occur on the upper shore. *U. rigida* occupies a wide zone and *Chaetangium erinaceum* appears on the shore above the *G. pristoides* belt which occupies the mid shore. Tufts of *Ceramium* sp. occur amongst the barnacles and the coralline *Jania* sp. is also present. In the lower balanoid zone lithothamnium and an algal turf encrust the rocks, barnacles and mussels. From this turf *Laurencia* sp., *Caulacanthus*, *G. minima*, *Amphiroa* sp., *Acrosorium* sp., *P. cloiophylla* and stunted *G. pristoides* have been identified, *Corallina* sp. is present and limited amounts of *Gigartina paxillata*, *Dictyota dichotoma* and *Hypnea spicifera* occur on the lower shore. *Cheilosporum cultratum*, *L. pumila/flexuosa* and *Plocamium corallorhiza* are abundant in the cochlear zone. *Ende-*

rachne binghamiae and *Caulacanthus* occur on the mid shore around the transect and *Sargassum heterophyllum* has been found in a nearby tidal pool. Diving has revealed that the shallow sublittoral is dominated by a turf form of *Laurencia* sp., red tufts of *Ceramium* sp. and *D. dichotoma* which are often attached to the tests of *Pyura*. Large plants of *Amphiroa ephedraea* and *Delisia flaccida* occur in deeper waters.

When the survey of the algae at Transect E (Fig. 7) was conducted in early February 1976 the upper shore was devoid of *P. capensis*. *L. semiplena*, *G. pristoides* and *Bryopsis* sp. occur on the mid shore and *Caulacanthus* has been found near the transect. *Gelidium paxillata* and *U. rigida* dominate the rest of the mid shore with *P. cloiophylla* abundant in the *Perna* zone of the lower shore. *Cheilosporum cultratum*, *P. corallorhiza*, *L. pumila/flexuosa*, *H. spicifera* encrusting lithothamnium and *Gelidium amansii* occur in the cochlear zone and *Gelidium cartilagineum* could be seen to be abundant on the sublittoral fringe.

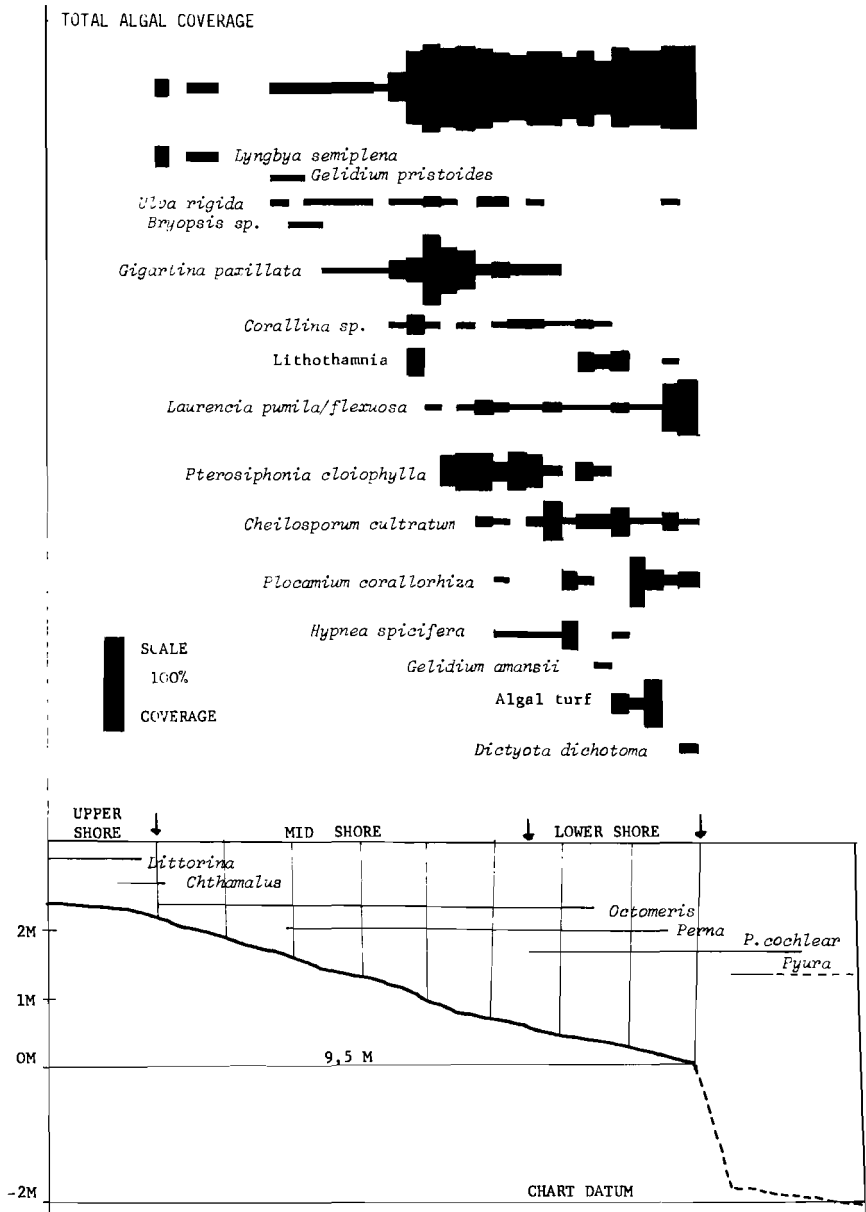


Fig. 7 Rocky shore profile, algal coverage and distribution of dominant animals at exposed Transect E.

Seasonal variations in the seaweed communities of St. Croix are evident from the diagram of percentage cover of algae at Transects S and M during summer and winter (Fig. 8). The upper shore algae that were present at Transect S in summer had disappeared by winter and although *U. rigida* was absent from the mid shore no major changes were evident for the rest of the shore. At Transect M the amount of *P. capensis* was markedly reduced in winter but *L. semiplena* was very abundant accounting for the large peak in quadrats 6 – 9. Again, no marked variation was evident for the rest of the shore. From the monthly observations during 1976 and 1977 the seasonal cycle of *P. capensis* became evident and this was particularly noticeable at Transect E where a settlement of tiny plants occurred in July 1976. In subsequent months these plants grew until by December large yellow-green plants were abundant. By January 1977 the amount of *P. capensis* had started to diminish and by March there were only few scattered plants in the vicinity of Transect E. During April and May there was no *P. capensis* on the shore but in June another settlement occurred. At Transect M a similar pattern was evident except that some *P. capensis* persisted throughout the

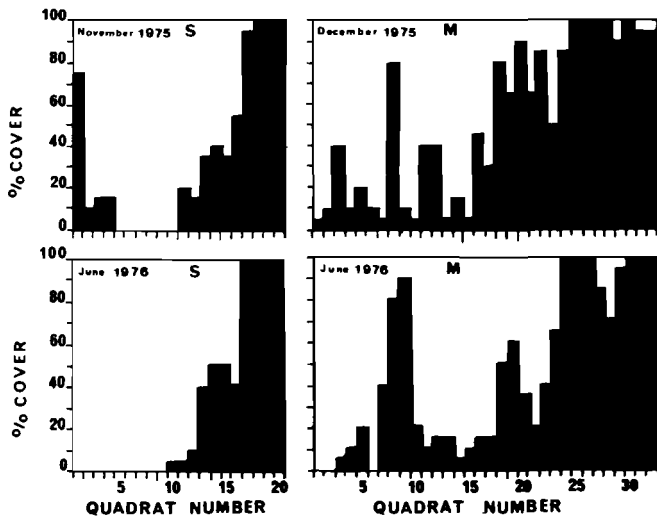


Fig. 8 Percentage coverage of algae in strip Transects S and M in summer 1975 and winter 1976.

autumn and early winter and the June 1977 settlement occurred whilst a few older plants were still attached to the rocks. At Transect S, *P. capensis* only occurs in isolated

tufts and young plants were observed in October 1976 and again in September 1977. *L. semiplena* at E followed the same pattern as at M being most abundant in autumn and early winter when *P. capensis* was least abundant. *Enteromorpha* sp. and *U. rigida* both appear to increase in abundance in late winter and spring.

The dry biomass of the dominant littoral seaweeds relative to percentage cover are given in Table 2. The coralline algae (*Cheilosporum*, *Corallina* and *Jania*) have a greater biomass to percentage cover ratio than the other littoral seaweeds because of their high ash content (Table 3). Energy values for 14 species of littoral algae are given in Table 3.

Table 2 Seaweed biomass relative to % coverage

Algae	% coverage/ 625 cm ²	Dry mass gm ⁻²
<i>Bryopsis</i> sp.	10	53,76
<i>Chaetangium erinaceum</i>	30	104,00
<i>Cheilosporum cultratum</i>	25	333,92
<i>Corallina</i> sp.	25	345,44
<i>Enteromorpha</i> sp.	50	37,76
<i>Gelidium pristoides</i>	80	397,76
<i>Gigartina paxillata</i>	50	405,12
<i>Hypnea spicifera</i>	25	73,92
<i>Jania</i> sp.	20	213,44
<i>Laurencia pumila</i>	15	41,44
<i>L. flexuosa</i>	30	132,80
<i>L. natalensis</i>	25	76,32
	40	122,08
<i>Lyngbya semiplena</i>	3,2	5,92
? <i>Lyngbya</i> sp.	1,6	2,56
<i>Plocamium corallorhiza</i>	15	30,32
<i>Porphyra capensis</i>	40	182,72
<i>Pterosiphonia cloiophylla</i>	35	113,28
Turf (Transect S)	0,8	6,08
Turf (Transect M)	4	11,52
<i>Ulva rigida</i>	25	49,12

Gelidium pristoides has the highest energy value (18,3 kJ/g dry mass) whilst the corallines exhibit very low energy values.

Discussion

The three transect sites in this study vary in exposure to wave action and consequently the macrobenthic plant and animal communities differ. The communities studied were representative of areas sheltered from, moderately exposed to and fully exposed to wave action. The south east cliffs (not sampled) which are exposed to extreme wave action are occupied by a community characterized by numerous *Octomeris angulosa*, *Perna perna* and *Pyura stolonifera*, very few upper and mid shore algae and a lower shore population of *Gelidium cartilagineum*. Ecotones between these four communities occur and a continuum of populations in response to environmental conditions is found in the littoral zone around St. Croix.

Octomeris angulosa is an indicator of areas which experience much water movement (Stephenson 1944; Field & McFarlane 1968) but is found on rocky shores right around St. Croix. This confirms the conclusion from the 'turbulometer' recordings that, despite transect S being sheltered from direct wave action, there is still considerable water movement. *Tetraclita serrata* is only abundant in sheltered areas but *Pyura stolonifera* occurs in greater numbers at the more exposed sites. *Perna perna* is more abundant at M and E than at S where the mussels occur interspersed among the barnacles and not in a distinct zone. The narrow *Littorina* zone at Transect E was surprising because spray can be felt 10 m above the intertidal on this shore but abrasion by penguins (*Spheniscus demersus*) is probably the cause of the limited population there.

Seaweeds on St. Croix can also be used as indicators of the extent of wave action. At sites sheltered from wave action algal turf consisting of both stunted and epiphytic seaweeds with much accumulated sediment and detritus covers most of the lower shore. Stephenson, Stephenson and Bright (1938) regard algal turfs as characteristic of

Table 3 Energy values and percentage ash for 14 littoral seaweeds

Algae	kJ/g (dry mass)	Standard deviation	% ash	kJ/g ash-free dry mass
<i>Chaetangium erinaceum</i>	16,760 ¹	0,289	8,3	18,275
<i>Cheilosporum cultratum</i>	1,838 ^{1,2}	0,155	81,5	9,935
<i>Corallina</i> sp.	1,824 ^{1,2}	0,343	79,8	9,119
<i>Enteromorpha</i> sp.	15,282	0,025	26,0	20,649
<i>Gelidium pristoides</i>	18,334	0,147	6,0	19,506
<i>Gigartina paxillata</i>	11,170 ¹	0,088	28,6	15,646
<i>Hypnea spicifera</i>	12,548	0,616	37,3	20,013
<i>Jania</i> sp.	2,998 ^{1,2}	0,255	72,6	10,940
<i>Laurencia pumilia/flexuosa</i>	11,551	0,021	36,2	18,104
<i>L. natalensis</i>	10,773	0,117	43,2	18,966
<i>Plocamium corallorhiza</i>	11,819	0,423	51,7	24,510
<i>Porphyra capensis</i>	16,216	0,172	14,4	18,937
<i>Pterosiphonia cloiophylla</i>	14,164	0,230	27,6	19,565
<i>Ulva rigida</i>	15,282	0,025	33,9	23,120

¹ Benzoic acid used in energy determination.

² Endothermy correction applied on assumption of 70% CaCO₃ content (Paine 1966).

rocky shores in the south coast region and they identified many of the constituent species. All the species do not occur in any one turf sample and some species may form tufts independent of the turfs thus making analysis of algal turfs difficult. On St. Croix *Gigartina paxillata* is an indicator of increased wave action and at Transect E it is very abundant with lesser quantities occurring at the moderately exposed Transect M. *Pterosiphonia cloiophylla* also occurs at exposed sites and the cochlear community of lithothamnium, *Cheilosporum cultratum*, *Plocamium corallorhiza* and *Laurencia pumila/flexuosa* is only abundant on more exposed shores.

The seasonal variation of seaweeds was most marked on the upper shores and the distinct seasonality of *Porphyra capensis* was very noticeable at Transect E where the old plants were removed in late summer, probably by the strong wave action. The settlement of the young gametophyte plants (see Graves 1955) on the bare rock was then obvious in the late winter and early spring.

The algal coverage estimations and percentage cover/biomass ratio make it possible to calculate the biomass of littoral seaweeds per area of shore without having to denude large areas of rocky shore and biomass values of up to 700 g dry mass/m² per species have been calculated for the St. Croix littoral zone. These biomass values per unit area of shore will be utilized for expressing seaweed epifauna standing stocks in a later paper.

Paine and Vadas (1969) concluded that the energy values of algae depend on phyletic affiliations, growth form, generation time, water purity, immersion depth and susceptibility to grazing. Although influenced by many factors, the energy content per gram dry mass of seaweed appear to be higher for the upper shore algae than for the lower shore algae on St. Croix.

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